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Higher system of Atalophlebiinae (Leptophlebiidae) with description of three new species of *Terpides* s.l. from Peruvian Amazonia

Общая система Atalophlebiinae (Leptophlebiidae) с описанием трёх новых видов *Terpides* s.l. из Перуанской Амазонии

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КЛЮЧЕВЫЕ СЛОВА: Ephemeroptera, Leptophlebiidae, Atalophlebiinae, Atalophleboadentata, Atalophlebopectinata, Atalophleboculata, Atalophlebomaxillata, Atalophlebolinguata, Calliarcyinae, Terpidinae, Castanophlebiinae, *Terpides*, новые виды.

ABSTRACT. There is suggested a new phylogenetic classification of the taxa, which in various non-phylogenetic ranking classifications can be named by a common name “subfamily Atalophlebiinae”; there are established new family-group taxa Calliarcyinae, Terpidinae and Castanophlebiinae **subfam.n.** and new taxa with non-typified circumscriptional names Atalophleboadentata, Atalophlebopectinata, Atalophleboculata, Atalophlebomaxillata and Atalophlebolinguata **taxa n.** Diagnosis of *Terpides* (= *Fittkaulus* **syn.n.**, = *Tikuna* **syn.n.**) is revised. Basing on material collected by the author in Peruvian Amazonia, there are described three new species: *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.** (as larvae and imagoes reared from larvae), *Terpides* (*Tikuna*) *nigrobulla* **sp.n.** (as larvae and male subimago reared from larva) and *Terpides* (*Tikuna*) *fusconotum* **sp.n.** (as male imago reared from subimago). Some larval characters for *Terpides* (*Tikuna*) *bilineata* are described for the first time. The species from Costa Rica, determined by Savage et al. [2005] as “*Tikuna atramentum*”, probably represents a new species, which here is discussed under an arbitrary name “*Terpides* (*Tikuna*) sp. SFP.

РЕЗЮМЕ. Предложена новая филогенетическая классификация таксонов, которые в различных нефилогенетических ранговых классификациях могут быть названы общим названием “подсемейство Atalophlebiinae”; установлены новые тасоны группы семейства — Calliarcyinae, Terpidinae и Castanophlebiinae **subfam.n.** и новые таксоны с нетипифицированными объёмными названиями — Atalophleboadentata, Atalophlebopectinata, Atalophleboculata, Atalophlebomaxillata и Atalophlebolinguata **taxa n.** Пересмотрен диагноз *Terpides* (= *Fittkaulus* **syn.n.**, = *Tikuna* **syn.n.**). На основе материала, собранного автором в Перуанской Амазонии описаны три новых вида: *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.** (по личинкам и имаго, выведенным из личинок), *Terpides* (*Tikuna*) *nigrobulla* **sp.n.** (по личинкам и самцу субимаго, выведенному из личинки) и *Terpides* (*Tikuna*) *fusconotum* **sp.n.** (по самцу имаго, выведенному из субимаго). Впервые описаны некоторые личиночные признаки *Terpides* (*Tikuna*) *bilineata*. Вид из Коста Рики, определенный Сэвэджем и др. [Savage et al., 2005] как “*Tikuna atramentum*”, вероятно, представляет собой новый вид; здесь он обсуждается под условным названием “*Terpides* (*Tikuna*) sp. SFP”.

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Introduction

This paper continues a series of publications whose aim is to bring in order system of Leptophlebiidae. Now it is used to divide the family Leptophlebiidae into many genera, whose number is nearly equal to the number of known species. Descriptions of these genera and species are in most cases rather detailed and accompanied by beautiful figures, but the most important characters remain to be non-described or described insufficiently.

Larval mouth apparatus is described and figured for each species, but on these figures mouth parts are shown together with all their setae, which are very dense and because of this can not be drawn adequately; so such important details as structure and position of dentisetae and constant setal rows appear to be non-described.

Most descriptions ignore such important character, as presence or absence of the patella-tibial suture; nearly for each species there is published a detailed figure of larval fore leg, but it does not contain necessary information, because in leptophlebiid larvae fore legs differ from middle and hind legs, and in all cases lack patella-tibial suture.

Most descriptions of larval coloration are meaningless, because the authors do not make difference between cuticular color (which exists only in larval stage and changes its intensity during each molting cycle) and hypodermal color (which passes through all larval instars to subimago and imago). Subimaginal cuticular pigmentation, being important in many cases, is described for a few species only.

Many taxa of leptophlebiids have tropical and notogean distribution, and for a long time I had no enough material of them; because of this, in the monograph on mayfly systematics [Kluge, 2004] system of leptophlebiids is omitted. The present paper is based on material, collected by me in Peru in 2006.

All material examined (including the holotypes of *Terpides amazonicus*, *T. fusconotum* and *T. nigrobulla* **spp.n.**) is deposited in the Zoological institute of Russian Academy of Sciences (in Saint-Petersburg), temporarily locates in Department of Entomology of Saint-Petersburg State University [Kluge, 1995]. The same is true for material from Peru described in my previous papers [Kluge, 2007, 2008], including the holotypes of *Oligoneuria itayana*, *Simothraulopsis sabalo*, *S. plesius* and *Hermanella chimaera*.

In the lists of material examined, the following arbitrary signs are used: L — larva; S — subimago; I — imago; L-S-I♂ — male imago reared from larva; L/S♂ — male subimago extracted from mature larva.

I. System of Atalophlebiinae and position of *Terpides*

Phylogenetic reconstruction should be based not on occasional combinations of characters (as in some calculations based on the non-scientific principle of parsimony), but on unique and conservative autapomorphies.

Overwhelming majority of Atalophlebiinae have the following features in mouthpart structure, not found in other taxa: maxilla lacks canines and has a single comb-like dentiseta directed apically; hypopharynx bears a pair of processes. These features are highly conservative, being retained in representatives with variously modified mouth apparates, independently of shape and specialization of maxillae and hypopharynx. The phylogenetic classification of Atalophlebiinae should be based on assumption that each of these characters appeared once and just after its appearance became conservative [Kluge, 2008]. According to this classification, the holophylum Leptophlebia/fg1 (corresponding to the family Leptophlebiidae in the generally accepted sense) is divided into (1) plesiomorphon Leptophlebia/fg2 (incl. *Paraleptophlebia* Lestage, 1917, *Neoleptophlebia* Kluge, 1997, *Habrophlebiodes* Ulmer, 1920) [f: Leptophlebini Banks, 1900; g: *Leptophlebia* Westwood, 1840] and (2) holophylum Atalophleboadentata. Detailed phylogenetic classification will be given in the website "Phylogeny of Ephemeroptera" [Kluge, web publication].

1. ATALOPHLEBOADENTATA, or Atalophlebia/fg1

Circumscriptional name: ATALOPHLEBOADENTATA Kluge, **taxon n.**

Hierarchical name: Atalophlebia/fg1 (incl. *Calliarcys*) [f: Atalophlebiinae Peters, 1980; g: *Atalophlebia* Eaton, 1881a].

Possible ranking name in non-phylogenetic classifications: subfamily Atalophlebiinae (in 1st, the widest sense).

Holophyletic taxon, characterized by an autapomorphy: maxillary canines are lost. The taxon Atalophleboadentata is divided into *Calliarcys* and Atalophlebopectinata.

1.1. *Calliarcys*

Circumscriptional name: absent.

Hierarchical name: Calliarcys/fg1 [f: Calliarcyinae Kluge, **subfam.n.**, type genus *Calliarcys*; g: *Calliarcys* Eaton, 1881b].

Possible ranking names in non-phylogenetic classifications: subfamily Calliarcyinae and genus *Calliarcys*.

Monospecific taxon, includes a single species *Calliarcys humilis* Eaton 1881, whose distribution is restricted by Iberian Peninsula.

1.2. ATALOPHLEBOPECTINATA, or Atalophlebia/fg2

Circumscriptional name: ATALOPHLEBOPECTINATA Kluge, **taxon n.**

Hierarchical name: Atalophlebia/fg2 (sine *Calliarcys*; incl. *Habrophlebia*).

Possible ranking name in non-phylogenetic classifications: subfamily Atalophlebiinae (in 2nd, wide sense).

Holophyletic taxon, characterized by the following autapomorphies:

(1) Proximal dentiseta has comb-like form (Fig. 1).

(2) Labrum has two transverse rows of setae.

The taxon Atalophlebopectinata is divided into Habrophlebia/fg1 and Atalophleboculata.

1.2.1. Habrophlebia/fg1

Circumscriptional name: absent.

Hierarchical name: Habrophlebia/fg1 (incl. *Habroleptoides*) [f: Habrophlebiinae Kluge, 1994; g: *Habrophlebia* Eaton, 1881a].

Possible ranking name in non-phylogenetic classifications: subfamily Habrophlebiinae.

Holophyletic taxon [Kluge, 1994]. Includes about 25 species, whose distribution is restricted by Holarctic.

1.2.2. ATALOPHLEBOCULATA, or Atalophlebia/fg3

Circumscriptional name: ATALOPHLEBOCULATA Kluge, **taxon n.**

Hierarchical name: Atalophlebia/fg3 (sine *Habrophlebia*; incl. *Terpides*).

Possible ranking name in non-phylogenetic classifications: subfamily Atalophlebiinae (in 3rd, medium sense).

Holophyletic taxon, characterized by the following autapomorphies:

(1) Upper portion of male eyes has square facets [Peters & Gillies, 1995].

(2) Stout setae on distal margin of labrum are lost.

The taxon Atalophleboculata is divided into Terpides/fg1 and Atalophlebomaxillata.

1.2.2.1. Terpides/fg1

Circumscriptional name: absent.

Hierarchical name: Terpides/fg1 (incl. *Fittkaulus* Savage & Peters, 1978, *Tikuna* Savage et al., 2005) [f: Terpidinae Kluge,

subfam.n., type genus *Terpides*; g: *Terpides* Demoulin, 1966].

Possible ranking name in non-phylogenetic classifications: subfamily Terpidinae.

In circumscription corresponds to "*Terpides* lineage": Savage, 1986.

Holophyletic taxon; includes 11 species, whose distribution is restricted by Neotropical Region (see below).

1.2.2.2. Atalophlebomaxillata, or Atalophlebia/fg4

Circumscriptional name: Atalophlebomaxillata Kluge, **taxon n.**

Hierarchical name: Atalophlebia/fg4 (sine *Terpides*; incl. *Castanophlebia*).

Possible ranking name in non-phylogenetic classifications: subfamily Atalophlebiinae (in 4th, narrow sense).

Holophyletic taxon, characterized by the following autapomorphy: distal dentiseta is lost. So maxilla, instead of initial three canines and two dentisetae, has a single comb-like dentiseta directed apically (it corresponds to the initial proximal dentiseta); in a few taxa, such as Hermanellognatha and *Choroterpides*, this dentiseta is also lost. The taxon Atalophlebomaxillata is divided into *Castanophlebia* and Atalophlebolinguata.

1.2.2.2.1. *Castanophlebia*

Circumscriptional name: absent.

Hierarchical name: Castanophlebia/fg1 [f: Castanophlebiinae Kluge, **subfam.n.**, type genus *Castanophlebia*; g: *Castanophlebia* Barnard, 1932].

Table. Characters of species in Terpides/fg1
Таблица. Видовые признаки в Terpides/fg1

Subgenera	*Terpides*			*Fittkaulus*		*Tikuna*					incertae sedis		
Species (asterisks indicate species examined)	*jessiae* [*Terpides*]	*guyanensis* [*Terpides*]	*diadema* [*Terpides*]	* *amazonicus* **sp.n.**	*maculatus* [*Fittkaulus*]	* *nigrobulla* **sp.n.**	* *bilineata* [*Choroterpes*]	* *fusconotum* **sp.n.**	*atramentum* [*Choroterpes*]	sp. SFP	*cuiabae* [*Fittkaulus*]	*curuensis* [*Fittkaulus*]	*vinculum* [*Choroterpes*]
larva:													
claw with enlarged distal denticle of inner-proximal row	+	+	+	–	–	–	–	?	?	?	?	?	?
fore femur with stout setae near inner margin	+	–	–	+	+	+	+	?	?	?	?	?	?
posterolateral spines on abdomere VI	+	+	–	+	?	–	–	?	?	?	?	?	?
denticles on tergum V	+	+	?	+	?	–	–	?	?	?	?	?	?
denticles on tergum VI	+	+	?	+	?	–	+	?	?	?	?	?	?
side projections on dorsal lamella of tergalii II–VI	–	–	–	+	+	+	?	?	?	?	?	?	?
side projections on ventral lamella of tergalii II–VI	–	–	–	–	–	+	?	?	?	?	?	?	?
fore wing:													
costal brace darkened	~	?	?	~	~	–	+	–	–	–	~	~	~
bulla with dark dot	~	?	?	~	~	+	–	–	–	–	~	~	~
apex of *sc* field yellow	–	?	?	–	–	+	+	+	+	+	–	–	–
maculae between RA and RS	+	?	?	+	+	–	–	–	+	+	+	+	+
macula in fork of MA	–	?	?	–	+	–	–	–	–	–	+	–	–
hypodermal color of legs:													
middle and hind femur with dark apical macula	+	?	?	+	–	–	–	–	–	–	+	+	?
hypodermal color of abdomen:													
tergum VIII with pair of convergenting stripes	–	?	?	–	–	+	+	–	+	+	–	–	–
male imago and subimago													
upper eyes of male high	–	?	?	–	+	–	–	–	–	–	?	?	?
number of distal segments of gonostylus	2	?	?	1	1	2	2	2	2	2	?	?	?
penes fused up to middle	+	?	?	+	+	+	?	+	+	–	?	?	?
penes side projections: shallow (±) or prominent (+)	–	?	?	–	–	+	?	±	+	+	?	?	?
penes apices with lateral projections	–	?	?	–	–	–	?	–	–	+	?	?	?
penes apices with long apical projections	–	?	?	+	–	–	?	–	–	–	?	?	?

Table legend: * species examined; + character present; – character absent; ~ character non-distinguishable or variable; ? character non-described; ? character unknown. Frames indicate subgeneric characters.

Легенда: * вид изучен; + признак имеется; – признак отсутствует; ~ признак неявственный или изменчив; ? признак не описан; ? признак не известен. Рамки обозначают признаки подродов.

Possible ranking names in non-phylogenetic classifications: subfamily Castanophlebiinae and genus *Castanophlebia*.

Holophyletic taxon. Includes 2 species, whose distribution is restricted by Ethiopian Region.

1.2.2.2.2. **Atalophlebolinguata, or Atalophlebia/fg5**

Circumscriptional name: Atalophlebolinguata Kluge, **taxon n.**

Hierarchical name: Atalophlebia/fg5 (sine *Castanophlebia*).

Possible ranking name in non-phylogenetic classifications: subfamily Atalophlebiinae (in 5th, the narrowest sense).

Holophyletic taxon, characterized by the following autapomorphy: hypopharynx has a pair of lateral processes. The taxon Atalophlebolinguata includes majority of Leptophlebiidae and has world-wide distribution.

DISCUSSION. W. Peters [1997] regarded the *Terpides* lineage and *Castanophlebia* to be sister groups and listed the following characters which he regarded to be their synapomorphies: (1) cross veins in cells C and Sc of hind wing crowded in middle of each cell under costal projection; (2) penes with a ventral rod or ridge; (3) styliger "dish-shaped" (posteromedian margin broad, concave; lateral margins extended); (4) larval claws with large median denticle. Actually, the structure of hind wing, which is characteristic for Terpides/fg1 and *Castanophlebia*, repeats in many non-related taxa of Leptophlebiidae; shape of penis is quite different in Terpides/fg1 (where it has similarity in all species) and in *Castanophlebia*; styliger is more or less concave in some other taxa [see, for example, Kluge, 2008: Figs 13, 18]; enlarged denticle on claw is present not in all Terpides/fg1, but in three species only, while in other 4 or 5 known species all denticles are subequal (see Table 1). Actually *Castanophlebia* belongs to a holophylum Atalophlebomaxillata, which does not include Terpides/fg1: as in other Atalophlebomaxillata, in *Castanophlebia* maxillae lack distal dentiseta, and mandibles are flattened, with outer margin widened and convex.

II. Characteristics and classification of Terpides/fg1

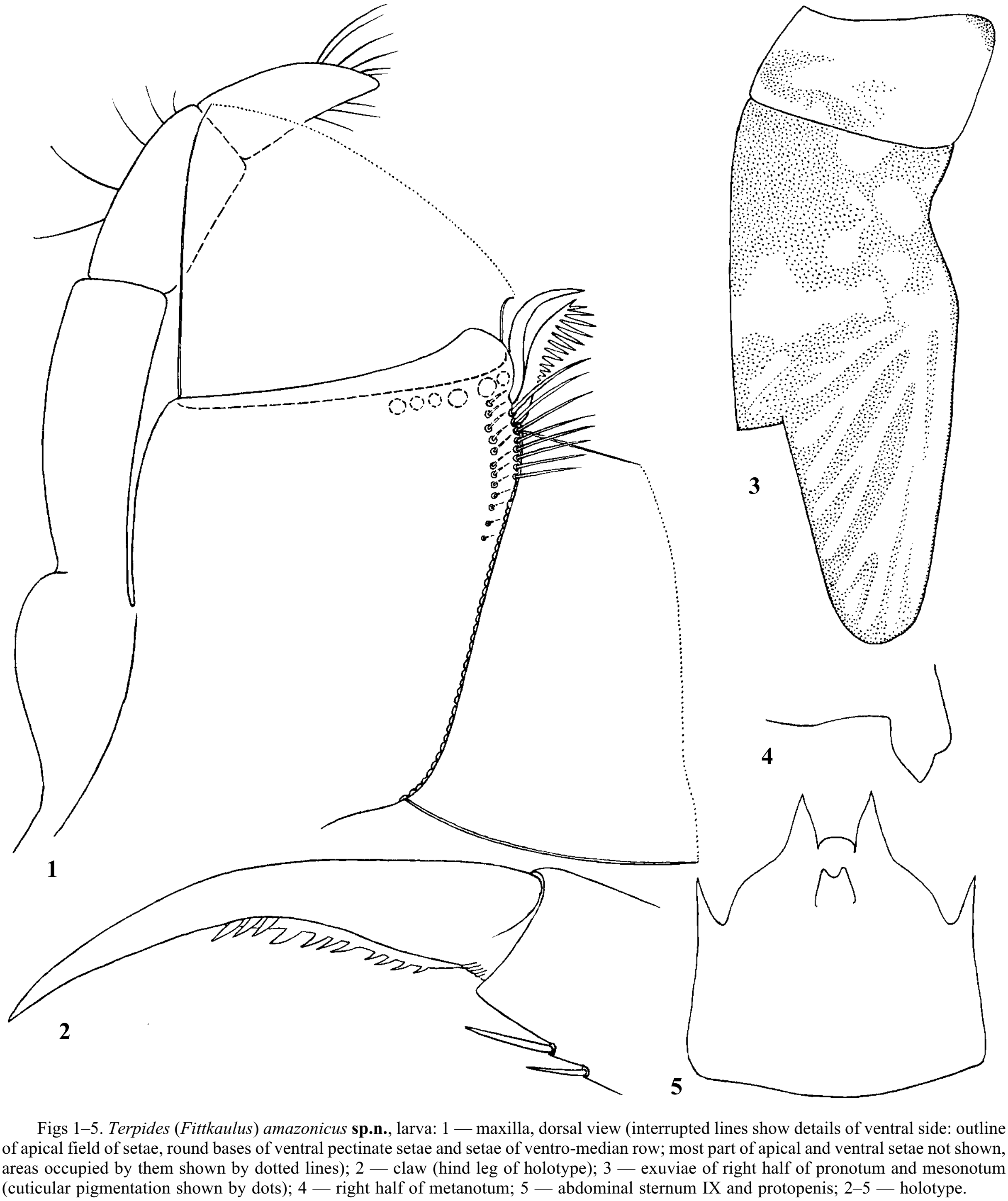
Larva. Head is more hypognathous than in most leptophlebiids. Labrum is narrower than clypeus, parallel-sided, with wide median emargination; both transverse setal rows locate near anterior margin [Peters & Harrison, 1974: Fig. 13]; at least in all three species examined these rows are irregular. Mandibles are more robust and have less convex outer margin than in Atalophlebomaxillata. Hypopharynx lacks lateral projections (unlike Atalophlebolinguata). Maxilla has a pectinate proximal dentiseta (typical for Atalophlebopectinata) and a simple distal dentiseta (unlike Atalophlebomaxillata); apical-ventral row of stout pectinate setae (characteristic for Leptophlebia/fg1) is short, consists of 6–7 pectinate setae only (Fig. 1). Labium: glossae have characteristic shape, curved over ventro-laterally. Stout pointed spine-like setae on inner margin of 3rd segment of labial palp form a single regular longitudinal row, that gives this segment serrate appearance. Fore femur (which in all leptophlebiids is more or less thickened basally, with outer margin convex basally) is much thicker than middle and hind femora and bears a regular longitudinal row of short, stout, pointed, spine-like setae on inner margin, that gives femur serrate appearance; other setae are situated irregularly [Peters & Harrison, 1974: Fig. 17]. Middle and hind femora are slender, parallel-sided, with irregularly situated setae only. Tibiae of all legs are slender; tibiae of middle and hind legs retain patella-tibial suture (unlike Neotropical taxon Hermanellonota and some Old World taxa). Abdominal segment VII always lacks posterolateral spines, while previous and next segments can have posterolateral spines (unlike other mayflies, whose posterolateral spines are not interrupted): posterolateral spines on segments VIII and IX are always present; on segment VI and more anterior segments posterolateral spines are either present, or absent. Caudalii have long secondary swimming setae: paracercus has clusters of long dense setae on lateral sides of each segment border, each cercus has such clusters on median side only (this setation superficially resembles siphlonuroud setation and functions in the same manner).

Subimago. On mesonotal cuticle, paired pigmented area, which is bordered by the mesonotal suture, is very narrow, in a form of a stripe along the medioparapsidal suture; posterior scutal protuberances are colorless and lacking microtrichiae. These features are well visible in species with intensive subimaginal cuticular pigmentation (Fig. 14); in species with colorless subimaginal cuticle, shape of pigmented areas is poorly visible, but is the same.

Subimago and imago. Fore wing has MA fork asymmetric (Figs 12, 13, 21, 24, 28) (plesiomorphy within leptophlebiids, autapomorphy of Leptophlebia/fg1); originally MA fork of *Terpides* was wrongly described as symmetric [Demoulin, 1966]. Hind wing is small, with prominent costal projection, Sc terminates just distad of costal projection and far from apex (Figs 12, 13, 21, 24) (the same in many non-related taxa). Tibiae of middle and hind legs retain patella-tibial suture (unlike Neotropical taxon Hermanellonota and some Old World taxa). On all legs both claws are pointed (apomorphy, independently appeared in several non-related mayfly taxa, while initial for Ephemeroptera are ephemeropteroid claws [Kluge, 2004]). On each gonostylus, the both distal segments are small, in some species fused forming a single segment. Penis lobes have slender apices brought together (Figs 15, 23, 26).

Classification of Terpides/fg1. Recently this taxon is regarded to be consisted of three genera: *Terpides* Demoulin, 1966, *Fittkaulus* Savage & Peters, 1978 and *Tikuna* Savage, Flowers & Porras, 2005. Each of these genera was originally established for a single species. Now the genus *Terpides* includes 4 species, among which only one species, *T. jessiae* Peters & Harrison, 1974, is known both as larvae and imagoes [Peters & Harrison, 1974; Boutonnet et al., 2004]; two species,

T. guyanensis Demoulin, 1966 and *T. diadema* Lugo-Ortiz & McCafferty, 1996, are known as larvae only [Demoulin, 1966; Boutonnet et al., 2004; Lugo-Ortiz & McCafferty, 1996]; one species, *T. vinculum* (Traver, 1947 [*Choroterpes*]), is known as female imago only [Traver, 1947] and has doubtful systematic position. The genus *Fittkaulus* includes 3 species, among which only one species, *F. maculatus* Savage & Peters, 1978, is known as larvae and imago [Savage & Peters, 1978], while two other species, *F. cuiabae* Savage, 1986 and *F. cururuensis* Savage, 1986, are known as female imagoes only [Savage, 1986] and have doubtful systematic



Figs 1–5. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.**, larva: 1 — maxilla, dorsal view (interrupted lines show details of ventral side: outline of apical field of setae, round bases of ventral pectinate setae and setae of ventro-median row; most part of apical and ventral setae not shown, areas occupied by them shown by dotted lines); 2 — claw (hind leg of holotype); 3 — exuviae of right half of pronotum and mesonotum (cuticular pigmentation shown by dots); 4 — right half of metanotum; 5 — abdominal sternum IX and protopenis; 2–5 — holotype.

Рис. 1–5. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.**, личинка: 1 — максилла, дорсально (прерывистыми линиями показаны детали на вентральной стороне: граница апикального поля щетинок, круглые основания вентральных гребенчатых щетинок и щетинки вентромедиального ряда; большая часть апикальных и вентральных щетинок не показана, занимаемые ими области показаны точечными линиями); 2 — коготок (задняя нога голотипа); 3 — экзувий правой половины пронотума и мезонотума (кутикулярнаяпигментация показана пунктировкой); 4 — правая половина метанотума; 5 — IX стернит брюшка и протопенис; 2–5 — голотип.

position. The genus *Tikuna* consists of two species, for one of which, *T. atramentum* (Traver, 1947 [*Choroterpes*]), larvae and imagoes are ascribed [Savage, Flowers & Porras, 2005], and another one, *T. bilineata* (Needham & Murphy, 1924 [*Choroterpes*]), is known as imagoes only [Needham & Murphy, 1924]. In the present paper 3 new species and some larval characters of *bilineata* [*Choroterpes*] are described. In spite of this, our knowledge about species composition of Terpides/fg1 remains to be too poor and does not allow to divide this small group into three or more subordinated taxa. It is most expedient to regard all known representatives of Terpides/fg1 as one genus, in order to avoid unnecessary changes of species binomina. Provisionally, this genus *Terpides* s.l. (= *Fittkaulus* **syn.n.**, = *Tikuna* **syn.n.**) can be divided into three subgenera, each characterized by a single character. Two of these characters (belonging to the subgenera *Fittkaulus* and *Tikuna*) are imaginal, and the third one (belonging to the subgenus *Terpides*) is larval. As larvae and imagoes are associated for 4 or 5 species only, we can not be sure that there are no species which combine characters of different subgenera.

The provisional classification suggested in the present paper, is the following.

The subgenus *Fittkaulus* can be characterized by a single apical segment of gonostylus (Fig. 15) (while in other taxa the both segments are retained). High eyes of male can not be included in the diagnosis of this taxon, because this character exists in a single species only. Here belong 2 species: *Terpides* (*Fittkaulus*) *maculatus* (Savage & Peters, 1978) **comb.n.** and *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.**

The subgenus *Tikuna* can be characterized by yellow apex of subcostal field of fore wing (while in other taxa there are brown or black maculae, but not yellow coloration) and, possibly, by presence of projections by sides of terminal filament on ventral lamella of tergalii II–VI (Fig. 17) (while in other taxa such projections are either absent, or present on dorsal lamellae only). Here belong 5 species: *Terpides* (*Tikuna*) *fusconotum* **sp.n.**, *Terpides* (*Tikuna*) *nigrobulla* **sp.n.**, *Terpides* (*Tikuna*) *bilineata* (Needham & Murphy, 1924 [*Choroterpes*]) **comb.n.**, *Terpides* (*Tikuna*) *atramentum* (Traver, 1947 [*Choroterpes*]) **comb.n.** and unnamed species *Terpides* (*Tikuna*) sp. SFP (= *Tikuna atramentum*: Savage, Flowers & Porras, 2005).

The subgenus *Terpides* s. str. can be characterized by enlarged apical denticle of inner row on larval claw (while in other taxa all denticles of the inner row and the subapical row have equal length). Here belong 3 species: *Terpides* (*Terpides*) *jessiae* Peters & Harrison, 1974, *Terpides* (*Terpides*) *guyanensis* Demoulin, 1966 and *Terpides* (*Terpides*) *diadema* Lugo-Ortiz & McCafferty, 1996.

Other species are known as female adults only and have uncertain systematic position: *Terpides cuiabae* (Savage, 1986 [*Fittkaulus*]) **comb.n.**, *Terpides cururuensis* (Savage, 1986 [*Fittkaulus*]) **comb.n.** and *Terpides vinculum* (Traver, 1947 [*Choroterpes*]) **comb.n.**

III. Species of *Terpides* from Peruvian Amazonia

1. ***Terpides* (*Fittkaulus*) *amazonicus*** Kluge, **sp.n.**
Figs 1–15

MATERIAL. Holotype: L-S-I♂ {specimen [XXIV](4)A}: PERU, Prov. Loreto, Quebrada El Sabalo — right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 9.II.2006, coll. N. Kluge. Paratypes: 1 L-S-I♀ {specimen [XXX](4)}, 1 ♀ subimago {specimen [XXIX](1)A}, 31 larvae, the same locality as holotype, 1–16.II.2006.

Larva. CUTICULAR COLORATION: Head, pronotum and mesonotum are light brown, with numerous distinctly outlined roundish blanks; among them characteristic blanks on mesonotum locate laterally-anteriorly and medially-posteriorly (Fig. 3). Fore legs are colorless; middle and hind legs are colorless, with brown band near tip of femur. Abdominal terga have contrasting light brown marks and lighter blanks, repeated on segments III–VIII (Fig. 8); among them there are characteristic paired submedian oblique light stripes on brown background; each tergum I–VII has a pair of dark brown spots near bases of tergalii. Caudalii unicolor.

HYPODERMAL COLORATION: Most part of body is light, with small contrasting dark brown markings; fore protoptera have maculae as on imaginal wings (Figs 12–13). Fore femora are either colorless, or have brown bands near base and near tip, or are entirely brown; middle and hind femora can have brown band near tip, as in imago. Abdomen can have brown markings as in imago (Fig. 11), including dark brown bands on posterior margins of terga, dark brown spots near bases of tergalii, transverse brown stripe on sternum I, lateral oblique brown stripes on sterna II–V and median anterior brown spot on some sterna.

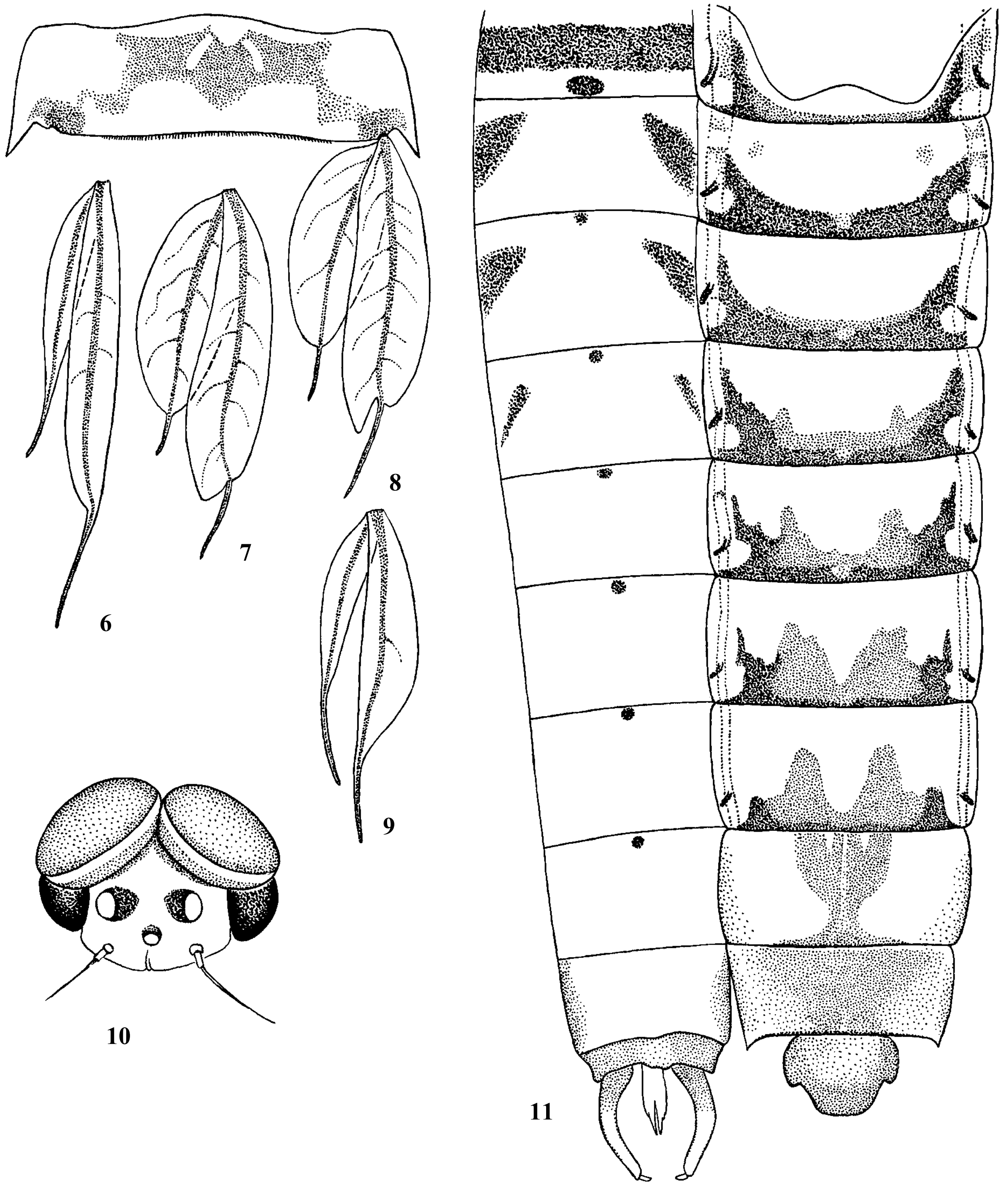
SHAPE AND SETATION: Maxilla has 6 (3+3) pectinate setae in the ventral-apical row (Fig. 1). Fore femur, besides a regular row of spine-like setae on inner margin and irregular pointed setae near outer margin (as in all Terpides/fg1), has serrate (but not pectinate) pointed setae, situated irregularly on anterior surface near inner margin. All denticles of claw are subequal (Fig. 2). On abdomen, posterolateral spines, besides segments VIII–IX, are present on segments V–VI and more anterior ones; on segments V–VI and VIII–IX they are subequal, long and pointed (Fig. 8); on segments II–IV they are less expressed, smaller and more blunt. Abdominal terga I–IV lack denticles on posterior margins; terga V–X have regular, long, pointed denticles on posterior margins (Fig. 8). Tergalius I is the longest, with dorsal lamella slightly widened, both lamellae lack projections by sides of the terminal filament (Fig. 6). Tergalii II–VI are subequal, with both lamellae widened; dorsal lamella has prominent projections by sides of the terminal filament; ventral lamella lacks such projections (Figs 7–8). Tergalius VII lacks projections by sides of the terminal filament (Fig. 9). Protopenis has apices widely separated (Fig. 5) (unlike imaginal penis).

Subimago. CUTICULAR COLORATION AND TEXTURE: Pronotum is light brownish. Mesonotum has contrasting dark brown markings on colorless background; the paired dark area bordered by mesonotal suture, is very narrow, in a form of a stripe along medioparapsidal suture; posterior scutal protuberances are partly brown, partly colorless (Fig. 14). Microtrichiae densely cover whole mesonotum except for posterior scutal protuberances; posterior scutal protuberances (both brown and colorless areas) lack microtrichiae. Ventral and lateral parts of thorax are colorless, with diffusive light

brownish maculation. Legs are colorless. Abdomen is light brownish with colorless, paired, submedian, oblique stripes on terga and sterna.

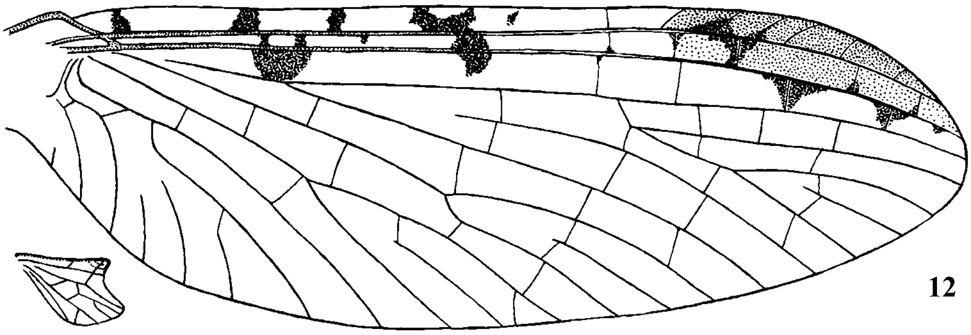
Hypodermal coloration: Color of legs and abdomen is as in imago.

Imago, male. Head is light brown. Upper portions of eyes are not high (Fig. 10), orange-brown, facetted surface are bordered by darker brownish; upper part of stem is light yellowish, lower part of stem is brown. Thorax is light brown with darker brown and lighter ocher maculation. On fore

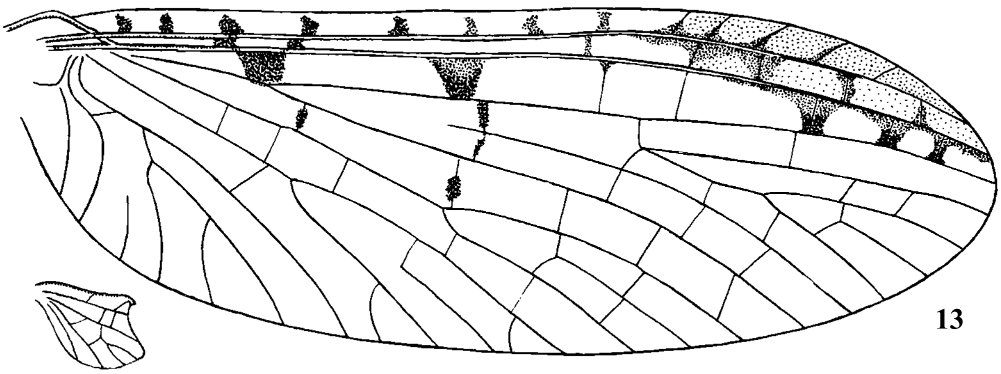


Figs 6–11. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.** (holotype): 6 — tergalius I; 7 — tergalius II; 8 — exiviae of abdominal tergum VI with tergalius (cuticular pigmentation shown by dots); 9 — tergalius VII; 10 — head of male imago; 11 — abdomen of male imago spread on slide (hypodermal pigmentation shown by dots).

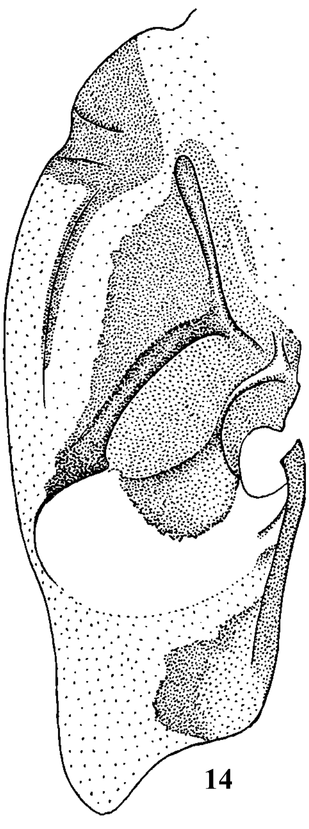
Рис. 6–11. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.** (голотип): 6 — тергалия I пары; 7 — тергалия II пары; 8 — эзувий VI тергита брюшка с тергалией (кутикулярная пигментация показана пунктировкой); 9 — тергалия VII пары; 10 — голова самца имаго; 11 — брюшко самца имаго, расправленное на препарате (гиподермальная пигментация показана пунктировкой).



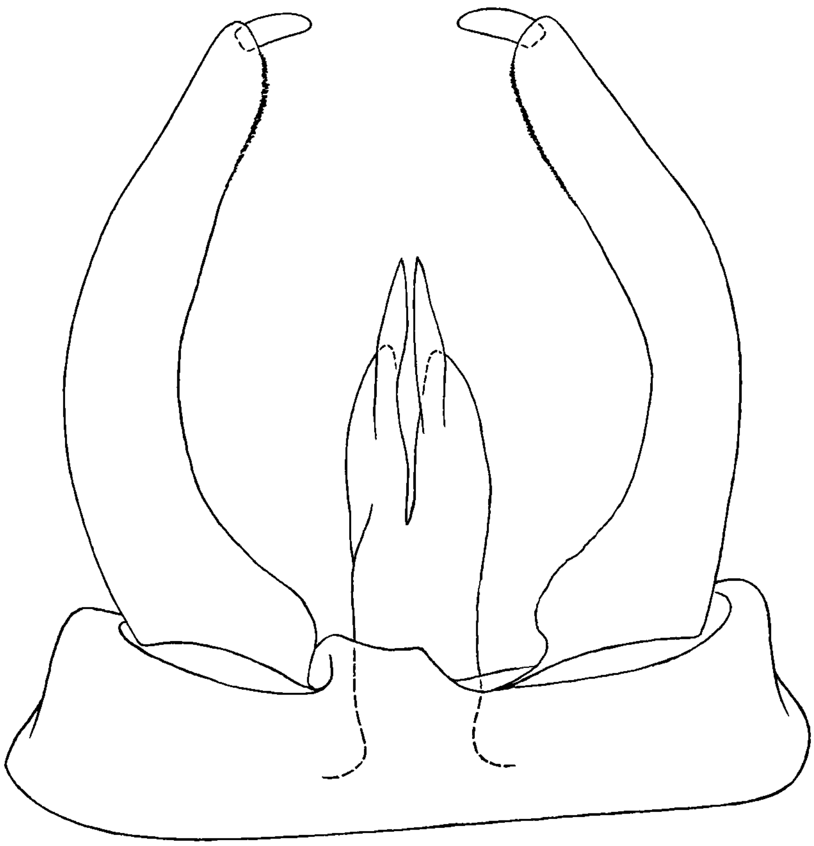
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14



15

Figs 12–15. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.**: 12–13 — fore and hind wings of different specimens; 14 — subimaginal exuviae of right half of mesonotum (cuticular pigmentation shown by dots); 15 — genitals of male imago; 12, 14–15 — holotype.

Рис. 12–15. *Terpides* (*Fittkaulus*) *amazonicus* **sp.n.**: 12–13 — переднее и заднее крылья разных экземпляров; 14 — субимагинальный экзувий правой половины мезонотум (кутикулярная пигментация показана пунктировкой); 15 — гениталии самца имаго; 12, 14–15—голотип.

wing, costal brace and proximal portions of Sc and RA are light brownish; other veins are light; pterostigmatic cross-veins are not anastomosed; there are contrasting dark brown or reddish maculae in costal, subcostal and radial fields (Fig. 12), in some specimens also in middle part of wing (Fig. 13). Hind wing has costal projection very prominent (Figs 12–13), colorless, with veins colorless. Fore leg: femur is entirely dark brown, tibia and tarsus are whitish, apex of tibia is slightly tinged with brown. Middle and hind legs: in most part are whitish, apical 1/5 of femur is dark brown. Abdomen whitish, with contrasting brown and reddish hypodermal maculation as in Fig. 11. Styliger and bases of gonostyli are light brownish, distal part of gonostyli and penis are yellowish. Each gonostylus has one distal segment only. Penis lobes in proximal half are fused, in distal half are divided and closely adjacent, apices are pointed (Fig. 15) (about larval protopenis see below). Caudalii are colorless.

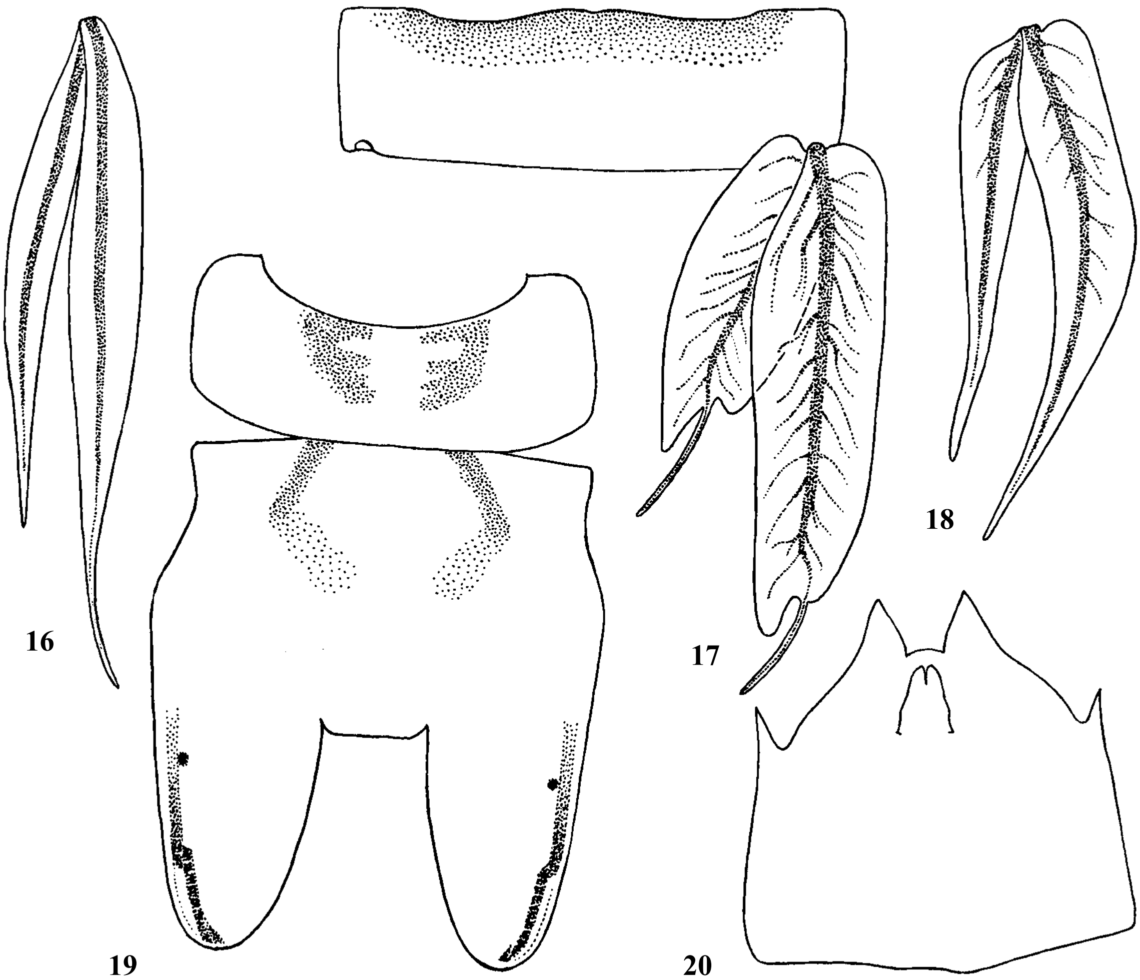
Imago, female. Head, thorax and abdomen are yellow, with contrasting brown maculation; maculation of abdomen is similar to that of male. Fore leg: femur is light brown, tibia and tarsus are whitish. Middle and hind legs: in most part are whitish, apical 1/5 of femur is light brown. Wings are as in male.

DIMENSION. Fore wing length 5 mm.

COMPARISON. Among species of *Terpides* s.l., besides *T. amazonicus* **sp.n.**, only *Terpides* (*Fittkaulus*) *maculatus* is known to have a single distal segment of gonostylus; in contrast to *T.* (*F.*) *maculatus*, in the new species upper portion of male imaginal eyes is not elongated, penes have long pointed apical projections, fore wings have no dark macula on MA furcation; larval claws of the new species are more slender than in *T.* (*F.*) *maculatus*.

2. ***Terpide*s (*Tikuna*) *nigrobulla*** Kluge, **sp.n.**
Figs 16–23

MATERIAL. Holotype: L-S♂ {specimen [XXIII](6)}: PERU, Prov. Loreto, Quebrada El Sabalo — right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 8.II.2006, coll. N. Kluge. Paratypes: 1 L/S♂, 1 L♀, the same locality as holotype, 1–16.II.2006.

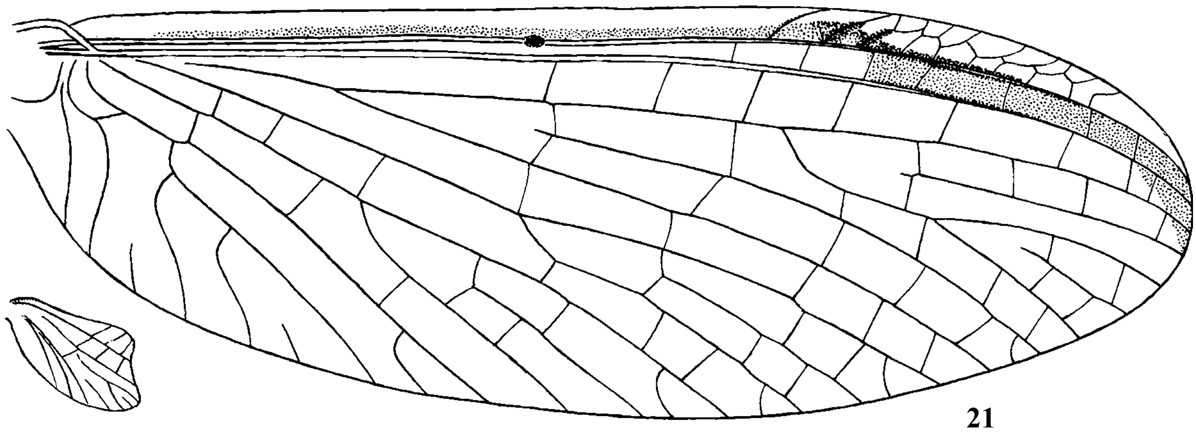


Figs 16–20. *Terpide*s (*Tikuna*) *nigrobulla* **sp.n.**, larva: 16 — tergalius I; 17 — exuviae of abdominal tergum VI with tergalius (cuticular pigmentation shown by dots); 18 — tergalius VII; 19 — pronotum and mesonotum (hypodermal pigmentation shown by dots; cuticular pigmentation not shown); 20 — abdominal sternum IX and protopenis; 20 — holotype.

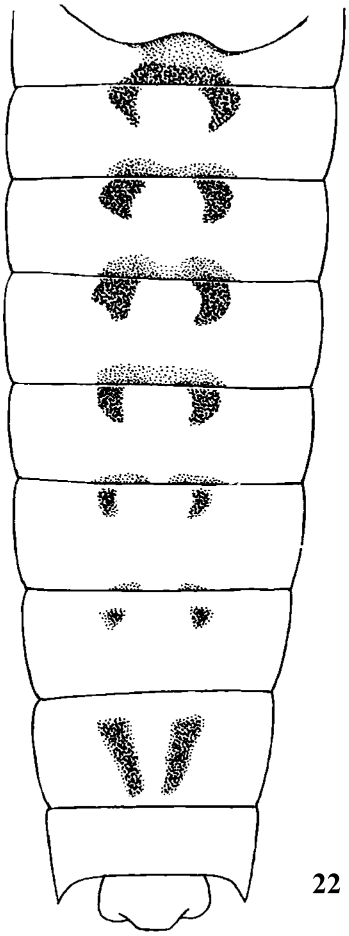
Рис. 16–20. *Terpide*s (*Tikuna*) *nigrobulla* **sp.n.**, личинка: 16 — тергалия I пары; 17 — экзувий VI тергита брюшка с тергалией (кутикулярная пигментация показана пунктировкой); 18 — тергалия VII пары; 19 — пронотум и мезонотум (гиподермальная пигментация показана пунктировкой; кутикулярная пигментация не показана); 20 — IX стернит брюшка и протопенис; 20 — голотип.

Larva. Cuticular coloration: Head, pronotum and mesonotum are brown, with diffusive blanks. All legs are colorless. Abdominal terga in most part are light, each tergum III–X has diffusive dark brown transverse band close to anterior margin (Fig. 17). Caudalii are unicolor.

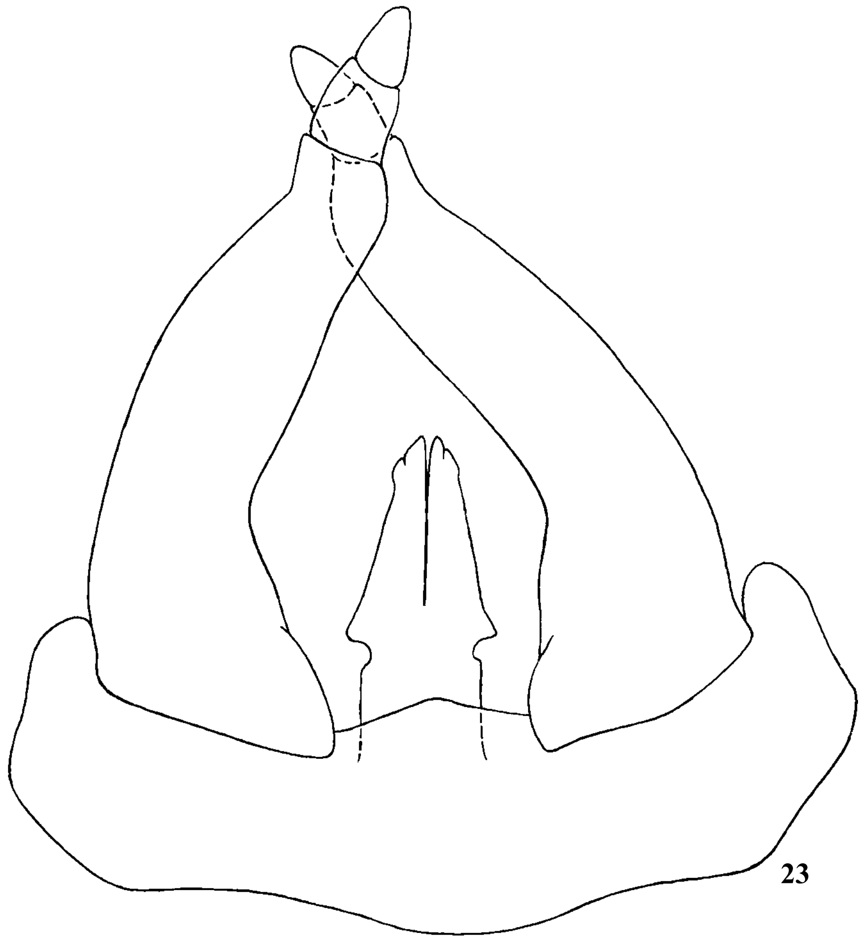
Hypodermal coloration: Most part of body is light, with small contrasting dark brown markings as in adult: pronotum has a pair of wide brown maculae (Fig. 19); mesonotum in anterior 1/3 has a pair of oblique brown stripes arising from anterior margin and diverging posteriorly (they correspond to imaginal anterolateral scutal crest); these stripes continue as lighter brown stripes converging posteriorly (they correspond to imaginal lateroparapsidal sutures) (Fig. 19); fore protoptera have intensive yellow or brownish stripes in proximal part of costal field and distal part of subcostal field (Fig. 19), as on adult wings. Legs are colorless. Abdomen has brown markings as in adult (as in Fig. 22): each tergum II–V has a pair of triangular brown maculae arising from anterior



21



22



23

Figs 21–23. *Terpides* (*Tikuna*) *nigrobulla* **sp.n.**, male subimago (holotype): 21 — fore and hind wings; 22 — abdominal terga spread on slide (hypodermal pigmentation shown by dots); 23 — subimaginal genitals.

Рис. 21–23. *Terpides* (*Tikuna*) *nigrobulla* **sp.n.**, самец субимаго (голотип): 21 — переднее и заднее крылья; 22 — тергиты брюшка, расправленные на препарате (гиподермальная пигментация показана пунктировкой); 23 — субимагинальные гениталии.

margin and converging posteriorly; terga VI–VII have similar, but smaller maculae; tergum VIII has a pair of longitudinal maculae converging posteriorly; terga XI–X lack hypodermal maculation. This coloration is identical in male and female.

SHAPE AND SETATION: Maxilla has 7 (4 lateral + 3 median) pectinate setae in ventral-apical row. Fore femur, besides a regular row of spine-like setae on inner margin and irregular pointed setae near outer margin (as in all Terpides/fg1), has bipectinate, stout, short setae, situated irregularly on anterior surface near inner margin. All denticles of claw are subequal. On abdomen, posterolateral spines are present on VIII and IX segments only, all segments I–VII lack posterolateral spines (Fig. 17). Abdominal terga I–VI lack denticles on posterior margins (Fig. 17) or have a few very small denticles only; terga VII–X have regularly, long, pointed denticles on posterior margins. Tergalius I is the longest, with dorsal lamella slightly widened, both lamellae lack projections by sides of the terminal filament (Fig. 16). Tergalii II–VI are subequal, with both lamellae widened; both dorsal and ventral lamellae have prominent projections by sides of the terminal filament (Fig. 17). Tergalius VII lacks projections by sides of the terminal filament (Fig. 18). Protopenis has apices brought together (Fig. 20).

Subimago. CUTICULAR COLORATION: Cuticle is entirely colorless.

HYPODERMAL COLORATION: Head is pale ocher, only bases of ocelli are dark brown. Upper portion of eyes have facetted surfaces light gray, stems dark brown. Pronotum is pale ocher, with a pair of large brown submedian maculae. Mesonotum is pale ocher, with anterolateral scutal crest dark brown, lateroparapsidal sutures are lighter brown. Metanotum has small brown markings. Thoracic sterna and pleura are pale ocher, without any brown markings. On fore wing, bases of C, Sc and RA and costal brace are colorless; oblique veins in proximal part of pterostigma are brown and bordered with brown; veins in distal part of pterostigma are light; other veins are light; membrane is colored by yellowish in proximal part of costal field and by intensive yellow in distal part of subcostal field; Sc has small dark brown dot on bulla (Fig. 21). Fore leg: femur is entirely orange-brown, tibia and tarsus are whitish. Middle and hind legs are entirely whitish. Abdominal terga are pale ocher, with contrasting, dark brown, paired, maculae on segments II–VIII: each tergum II–V has a pair of triangular brown maculae arising from anterior margin and converging posteriorly; terga VI–VII have similar, but smaller maculae; tergum VIII has a pair of longitudinal maculae converging posteriorly; terga XI–X lack hypodermal maculation (Fig. 22). Abdominal sterna are pale ocher, without any maculation.

SHAPE: Hind wing has moderately prominent costal projection (Fig. 21). Penis lobes in proximal half are fused, in distal half divided and closely adjacent, apices are incised, lateral sides have a pair of sharp projections directed laterally-basally (Fig. 23).

Imago. Unknown.

DIMENSION. Fore wing length 6 mm.

COMPARISON. The new species is similar to *bilineata* [*Choroterpes*] (see below): it also has pale body with a pair of longitudinal blackish dorsal stripes and the same yellow stripe on fore wing. In contrast to *bilineata* [*Choroterpes*], whose "humeral cross vein deep blackish brown" (Fig. 28), the new species has the cross portion of costal brace colorless (Figs 20–21). Comparison of the new species with the larva from Itaya, determined by me as *T. bilineata*, reveals that it differs also by shape of hypodermal markings which form a pair of longitudinal dorsal stripes along the body: in *T. nigrobulla* **sp.n.** stripes of anterior part of mesonotum are diverging posteriorly (Fig. 19), while in *T. bilineata* they are converging posteriorly (Fig. 28); in *T. nigrobulla* stripes are progressively shorter on abdominal terga II–VII (Fig. 22), while in *T. bilineata* stripes are progressively longer on abdominal terga II–VIII (Fig. 27). Larva of *T. nigrobulla* differs from larva determined as *T. bilineata* also by presence of dark cuticular coloration of anterior parts of abdominal terga and by absence of long denticles on posterior margin of tergum VI (Fig. 17).

The new species is also similar to *atramentum* [*Choroterpes*], which was described as male and female subimagoes [Traver, 1947]: it has the same color of body, the same yellow stripe on fore wing, colorless costal brace and similar shape of penis [Savage et al., 2005: Fig. 13]. From *atramentum* [*Choroterpes*] the new species differs by absence of brown spots in costal and radial fields of fore wing.

3. ***Terpides* (*Tikuna*) *fusconotum*** Kluge, **sp.n.**
Figs 24–26

MATERIAL. Holotype: S-I♂: PERU, Prov. Loreto, collected at light near Quebrada El Sabalo — right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 1–16.II.2006, coll. N. Kluge.

Larva. Unknown.

Subimago. CUTICULAR COLORATION AND TEXTURE: Subimaginal cuticle is entirely colorless. Areas of mesonotum have the same outlines as in *T. amazonicus* (as in Fig. 14); microtrichiae densely cover whole mesonotum except for posterior scutal protuberances, which lack microtrichiae.

HYPODERMAL COLORATION: as in imago.

Imago, male. Head dorsally is dark brown, face is pale ocher. Upper portions of eyes are not high, facetted surface is yellowish, stem brown. Pronotum, mesonotum and metanotum have cuticle brown; under cuticle, there is visible a hypodermal coloration: a pair of large dark brown maculae on pronotum and dark brown anterolateral scutal crest. Pleura and sterna of thorax are pale ocher; cuticle of episterna of mesothorax and metathorax is tinged with brown. On fore wing, bases of C, Sc and RA are light brown; costal brace is colorless; proximal portions of Sc and RA are yellowish; oblique veins in proximal part of pterostigma are non-anastomosed, brown and bordered with brown; veins in distal part of pterostigma are light and anastomosed; other veins light; membrane is colored by yellowish in proximal part of costal field and by intensive yellow in distal part of subcostal field; there are no brown dots in area of bulla (Fig. 24). Hind wing has moderately prominent costal projection, Sc is light brownish, other veins are colorless. Fore leg: femur is entirely orange-brown, tibia and tarsus are whitish. Middle and hind legs are entirely whitish. Abdomen is ocher, laterally pale, ventrally darker, dorsally the darkest; terga have light brown bands on posterior margin; each tergum I–VII has a pair of brown spots near posterior margin; tergum VIII has a large rectangular spot which occupies the most its part; terga IX–X lack brown spots (Fig. 25). Styliger and gonostyli are light brownish. Each gonostylus has two distal segment. Penis lobes in proximal half are fused, in distal half are divided and closely adjacent, apices are incised, lateral sides have a pair of shallow protuberances (Fig. 26). Caudalii are colorless.

DIMENSION. Fore wing length 5 mm.

COMPARISON. Among species with yellow stripe in distal part of subcostal field, the new species *T. fusconotum* differs from *T. bilineata*, *T. atramentum*, *T. nigrobulla* **sp.n.** and *T.* sp. SFP by color of abdominal tergum VIII, which has an integral dark brown macula instead of a pair of converging

longitudinal stripes; in contrast to these species, imago of *T. fusconotum* has entirely brown thoracic nota. Besides this, in *T. fusconotum* paired dark maculae on terga II–VII are close to hind margins of terga, while in *T. nigrobulla* **sp.n.** and *T.* sp. SFP paired maculae on terga II–VII are close to fore margins of terga, and in *T. bilineata* they are more elongate. *T. fusconotum* also differs from *T. nigrobulla* **sp.n.** by absence of brown dot on bulla. Penis of *T. fusconotum* has less prominent lateral protuberances, than in *T. nigrobulla* **sp.n.**, *T. atramentum* and *T.* sp. SFP.

4. ***Terpide*s (*Tikuna*) *bilineata*** (Needham & Murphy, 1924), **comb.n.**

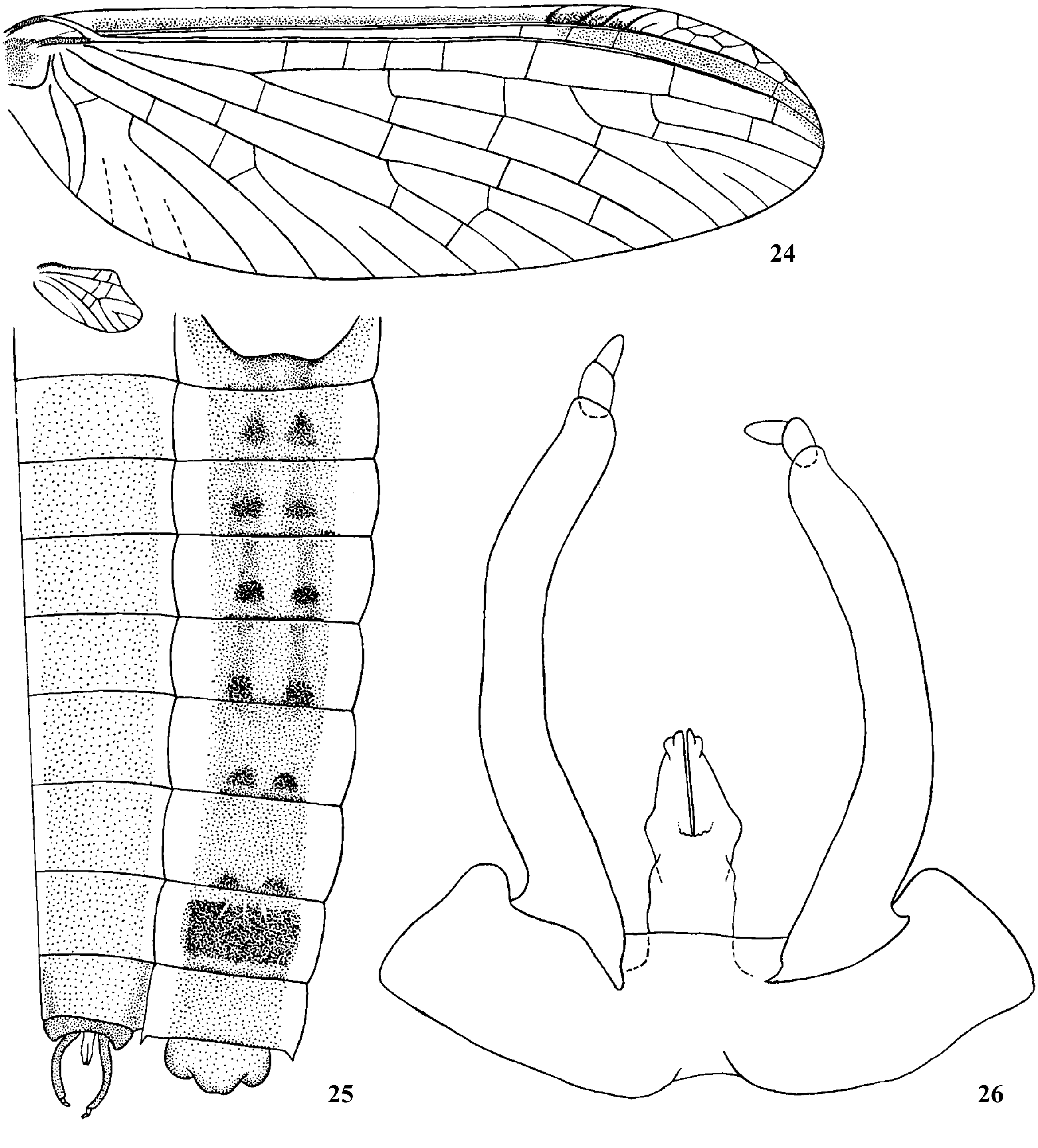
Figs 27–28

Choroterpes bilineata Needham & Murphy, 1924.

Tikuna bilineata: Peters et al., 2005.

MATERIAL. PERU, Prov. Loreto, Rio Itaya at Puente Itaya (57 km by road from Iquitos), 1–16.II.2006, coll. N. Kluge: 1 ♀ larva (without tergalii).

Larva. CUTICULAR COLORATION: Cuticle of head, thorax, abdomen, legs and caudalii is nearly colorless, only with a few indistinct diffusive darker markings.



Figs 24–26. *Terpide*s (*Tikuna*) *fusconotum* **sp.n.**, male imago (holotype): 24 — fore and hind wings; 25 — abdomen spread on slide (hypodermal pigmentation shown by dots); 26 — genitals.

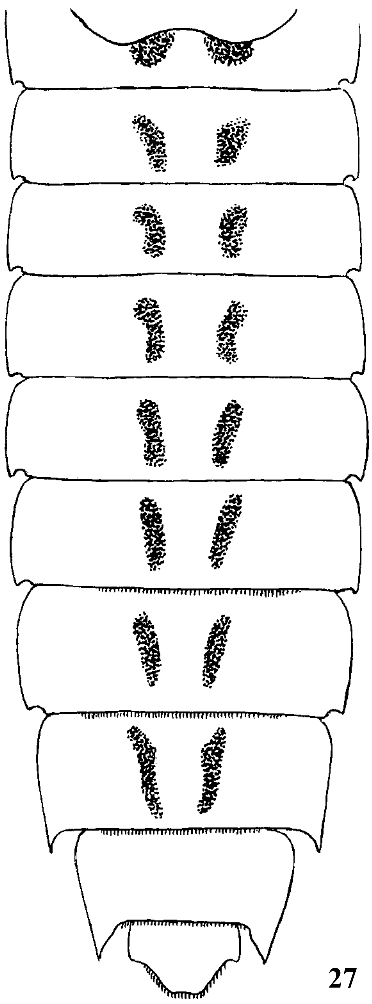
Рис. 24–26. *Terpide*s (*Tikuna*) *fusconotum* **sp.n.**, самец имаго (голотип): 24 — переднее и заднее крылья; 25 — брюшко, расправленное на препарате (гиподермальная пигментация показана пунктировкой); 26 — гениталии.

Hypodermal coloration: Most part of body is light, with small contrasting dark brown markings as in adult: pronotum has a pair of wide brown longitudinal stripes (Fig. 28); mesonotum in anterior 2/3 has a pair of oblique brown stripes arising from anterior margin and converging posteriorly (Fig. 28); fore protoptera have intensive color as on imaginal wing: reddish-brown stripes in proximal part of costal field and distal part of subcostal field; costal brace, proximal part of costal vein and crossveins in base of pterostigma are margined with dark brown (Fig. 28). Legs are colorless. Abdomen has brown markings (Fig. 27): tergum I has a pair of short brown maculae; each tergum II–VIII has a pair of longitudinal brown maculae converging posteriorly and becoming longer from tergum II to tergum VIII; terga XI–X lack hypodermal maculation.

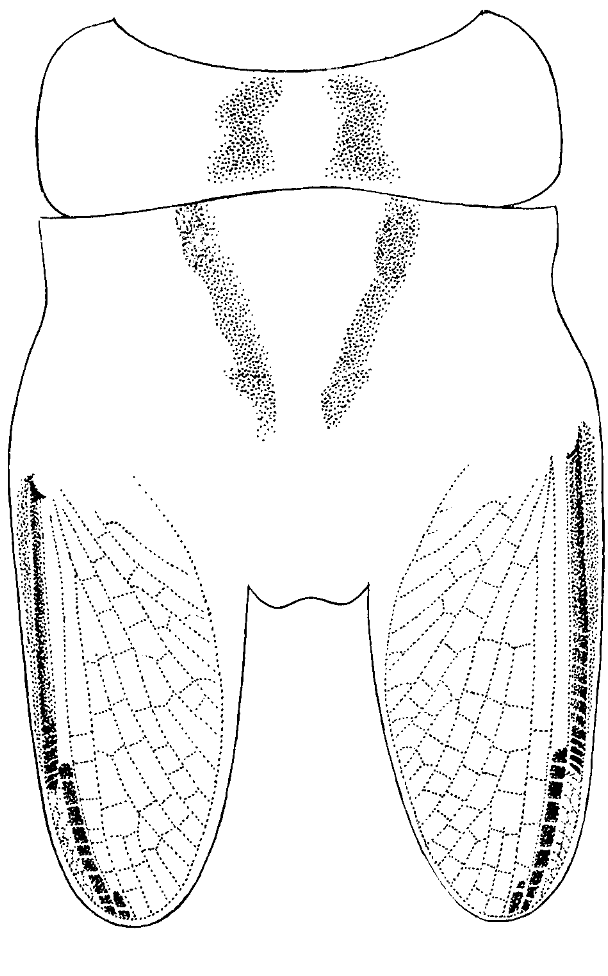
Shape and setation: Maxilla has 7 (4 lateral + 3 median) pectinate setae in ventral-apical row. Fore femur, besides a regular row of spine-like setae on inner margin and irregular pointed setae near outer margin (as in all Terpides/fg1), has bipectinate, stout, short setae, situated irregularly on anterior surface near inner margin. All denticles of claw are subequal. On abdomen, posterolateral spines are present on VIII and IX segments only, all segments I–VII lack posterolateral spines (Fig. 27). Abdominal terga I–V lack denticles on posterior margins; terga VI–X have regularly, long, pointed denticles on posterior margins (Fig. 27).

COMMENTS. This species was originally described from Putumayo district of Peru as female imagoes and male subimagoes [Needham & Murphy, 1924]. Subimaginal genitals were figured only by Traver [1947], but this figure is not enough detailed. In the same paper Traver described "a female imago which seems to be of this species" from Surinam, which differs from the type specimen by presence of 10 small brown spots at costal field of fore wing. Judging by the fact that there are several species with similar coloration, this female imago, most probably, belongs to an undescribed species.

The single larva from river Itaya, is identified by me as *bilineata* [*Choroterpes*], basing on its hypodermal color of



27



28

Figs 27–28. *Terpide*s (*Tikuna*) *bilineata*, larva: 27 — abdominal terga spread on slide (hypodermal pigmentation shown by dots, cuticular pigmentation not shown); 28 — pronotum and mesonotum spread on slide (hypodermal pigmentation shown by dots, cuticular pigmentation not shown; veins shown by dotted lines, but actually they are lighter than background).

Рис. 27–28. *Terpide*s (*Tikuna*) *bilineata*, личинка: 27 — тергиты брюшка, расправленные на препарате (точками показана гиподермальная пигментация, кутикулярная пигментации не показана); 28 — пронотум и мезонотум, расправленные на препарате (точками показана гиподермальная пигментация, кутикулярная пигментации не показана; жилки показаны точечными линиями, но на самом деле они светлее фона).

body and protoptera, which in all other species of *Terpides* are identical to imaginal color of body and wings.

5. *Terpides* (*Tikuna*) sp. SFP

Tikuna atramentum: Savage, Flowers & Porras, 2005 (non Traver, 1947).

Savage et al. [2005] believed that the specimens described by them from Costa Rica, belong to *atramentum* [*Choroterpes*], because thay have the same maculation on body and wings. As we can see from comparison of specimens from Peru, in this group of mayflies quite similar color pattern occurs in different species. Male imago, described by Savage et al. [2005], has unusual shape of hind wing [Savage et al., 2005: Figs 1 and 2], its penis lobes are separated up to base and have subapical protuberances projected laterally [Savage et al., 2005: Figs 11 and 12]. In contrast to it, male subimago of *atramentum* [*Choroterpes*] has more usual shape of hind wing [Savage et al., 2005: Figs 5 and 6] and penis lobes separated up to middle and lacking subapical protuberances [Savage et al., 2005: Fig. 13]. The same in subimago of the new species *T. nigrobulla* (Figs 21, 23). These differences can not be connected with stage of development: wing shape of imago and subimago is identical in all mayflies, and penis shape in imago and subimago is similar in most leptophlebiids. It is unclear, to which species, to sp. SFP, or to true *atramentum* [*Choroterpes*], belong larvae described by Savage et al. [2005] under the name "*Tikuna atramentum*", because they had no reared material and did not use other reliable method of associating larvae and imagoes.

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